

Space Use and Habitat Selection by Bobcats in the Fragmented Landscape of South-Central Iowa

STEPHANIE A. TUCKER, *Department of Ecology, Evolution and Organismal Biology, Iowa State University, 253 Bessey Hall, Ames, IA 50011, USA*

WILLIAM R. CLARK,¹ *Department of Ecology, Evolution and Organismal Biology, Iowa State University, 253 Bessey Hall, Ames, IA 50011, USA*

TODD E. GOSELINK, *Chariton Research Station, Iowa Department of Natural Resources, 24570 US Highway 34, Chariton, IA 50049, USA*

ABSTRACT Historically, bobcats (*Lynx rufus*) were found throughout the Corn Belt region, but they nearly disappeared from this area due to habitat loss and unregulated harvest that occurred during the century after European settlement. Reports of bobcat occurrences have been increasing in Iowa, USA, and biologists would like to understand the mechanisms enabling bobcats to recolonize this fragmented agricultural landscape. We determined space use and habitat selection of bobcats by radiocollaring 68 bobcats in south-central Iowa during 2003–2006. We triangulated 12,966 locations and recovered an additional 1,399 3-dimensional locations from Global Positioning System collars. We used a fixed kernel estimator to calculate 95% utilization distributions (UDs) for home ranges and 50% UD for cores. Annual home range area of males (\bar{x} = 58.6 km², 95% CI = 49.2–69.9) was nearly 3 times that of females (\bar{x} = 19.9 km², 95% CI = 17.0–23.3). Females used smaller home ranges during April–September when they were suspected to have kittens with them (\bar{x} = 16.8 km², 95% CI = 13.7–20.7), as compared to October–March (\bar{x} = 24.1 km², 95% CI = 19.0–30.7), whereas home ranges of males did not differ between seasons. Similarly, core area of males (\bar{x} = 7.7 km², 95% CI = 6.2–9.6) was larger than that of females (\bar{x} = 2.3 km², 95% CI = 1.9–2.7). Females used significantly smaller cores in April–September (\bar{x} = 1.8 km², 95% CI = 1.4–2.3) as compared to October–March (\bar{x} = 2.8 km², 95% CI = 2.2–3.7), whereas males did not. For both sexes, compositional analysis indicated that forest habitat was ranked higher than all other habitat classes at both the landscape and local scale. Standardized habitat selection ratios illustrate that female and male bobcats selected forest habitat about twice as frequently as any other habitat class, including grassland and Conservation Reserve Program land. Predictive models indicated that home range and core area was smaller in landscapes where perennial forest and grassland habitats were less fragmented. Predictive models indicated home ranges were more irregular in shape in landscapes where row crop patches were less aggregated within home ranges. Our results have practical implications for wildlife managers regarding expected bobcat habitat use and distribution as the species becomes more abundant in the agricultural landscape of the Midwest. (JOURNAL OF WILDLIFE MANAGEMENT 72(5):1114–1124; 2008)

DOI: 10.2193/2007-291

KEY WORDS bobcat, habitat selection, home range, Iowa, landscape, *Lynx rufus*.

Historically, bobcats (*Lynx rufus*) were widespread in the prairie woodland complexes of the Midwest, but during the century after European settlement (1840s–1940s) they were considered rare throughout the Corn Belt region (Deems and Pursley 1978, Dinsmore 1994). The disappearance of bobcats from this region has been attributed primarily to unregulated harvest and to an increase in the amount of land converted to agriculture (Rolley 1987, Woolf and Hubert 1998). In 1977 the Department of Natural Resources (DNR) listed the bobcat as Endangered in Iowa, USA. Around that same time bobcats also became protected in Illinois (Protected in 1972; Threatened in 1977), Indiana (Endangered in 1969), and Ohio (Endangered in 1974), USA. Since then, periodic reports of presence of bobcats in Iowa have occurred, with a dramatic increase in these reports since the early 1990s. These reports resulted in changing the status from Endangered to Threatened and then to Protected, with no open season, by 2003. The increase of bobcats in Iowa is consistent with other areas of the Midwest (Woolf and Hubert 1998). Like other populations of large predators in altered landscapes (Maehr et al. 2001, Sunquist and Sunquist 2001), there is considerable interest in understanding the response of bobcats to habitat fragmentation and configuration that is enabling them to persist and expand in the Midwest.

Iowa is well known for having an agriculturally dominated landscape consisting of almost 60% annual row crops.

Preferred bobcat habitats such as forest (Hall and Newsom 1976, Rucker et al. 1989, Lovallo and Anderson 1996, Nielsen 2000) and grassland (Kamler and Gipson 2000) occur in a fragmented mosaic of patches and corridors in Iowa (Kane et al. 2002) that may affect bobcats by limiting their movements, altering home range boundaries, and modifying habitat selection patterns (Sunquist and Sunquist 2001). Previous studies of bobcat habitat selection have been conducted in areas such as Wisconsin (Lovallo and Anderson 1996), Michigan (Preuss and Gehring 2007), and Mississippi (Chamberlain et al. 2003), USA, where large, continuous areas of forest are widespread, although Kamler and Gipson (2000) showed that bobcats selected grassland over forest in Kansas, USA. In recent decades the enrollment of land into the Conservation Reserve Program (CRP) may have led to increases in the amount of potential habitat available to bobcats and their prey, so it is reasonable to suggest that CRP lands could be important to the population ecology of bobcats in Midwestern landscapes.

A fundamental motivation for our research was to understand habitat occupancy that would help to predict expansion into the agriculturally dominated landscape of Iowa. Our analyses focused first on examining the sex-specific space use of bobcats and then estimating habitat selection ratios at multiple orders to determine the relative importance of habitat types to the species in Iowa. Ultimately, our goal was to create models that predict the area and shape of the home range so that we might gain

¹ E-mail: wrclark@iastate.edu

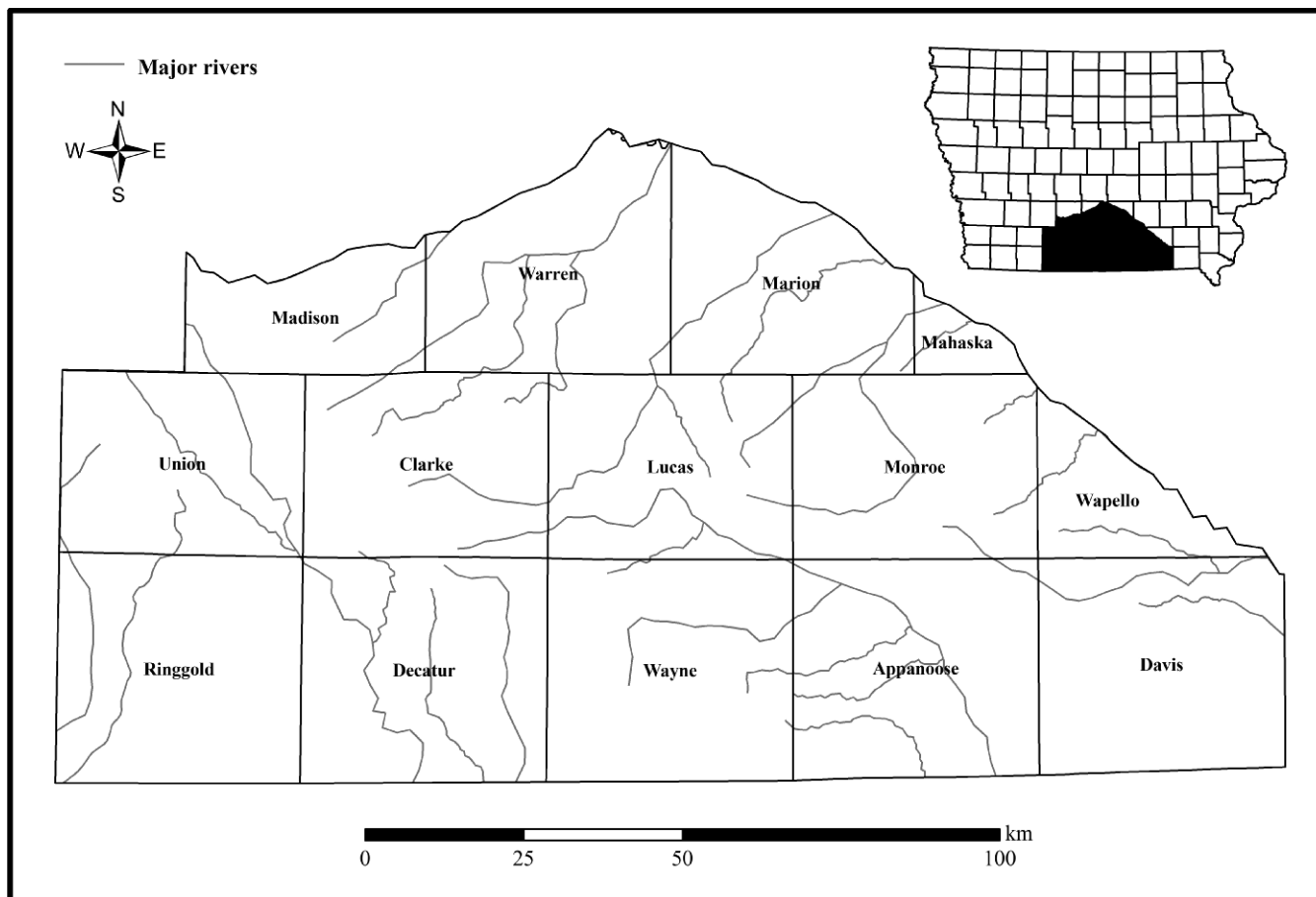


Figure 1. Location of our study area in south-central Iowa, USA, where we radiocollared bobcats in 2003–2006. The major rivers were delineated by the Iowa Department of Natural Resources, Geological Survey, 1997.

insights into the effects of fragmentation on bobcat habitat use and configuration. Predicting home range area is a rudimentary way to calculate density in various landscapes, in light of the territorial land tenure social structure of bobcats (Anderson 1987, Sunquist and Sunquist 2001, Diefenbach et al. 2006). We viewed shape as an index to the response of bobcats to the fragmentation and configuration of habitat elements. In other words, we hypothesized that home ranges might be elongated along linear habitat elements or more convoluted where habitat is more fragmented (Frey and Conover 2006). Our habitat selection modeling focused on the habitat features, in addition to forest composition, that were important in predicting space use by bobcats.

STUDY AREA

We trapped and radiocollared bobcats in a 25,043-km² area in south-central Iowa containing all or portions of 14 counties (Fig. 1). We chose this area because its proportion of forest habitat was greater than anywhere else in Iowa, because it had the largest number of reported bobcat sightings and incidentally trapped bobcats prior to our study, and for logistical reasons. The study area boundary consisted mainly of county lines; however, we did not include areas north of the Middle and Des Moines rivers, which we viewed as potential barriers to bobcat movements (Koehler

2006). The major habitat types in our study area were grasslands and pastures (44%), row crops consisting primarily of corn and soybeans (22%), forest (16%), and CRP (13%). Mean road density, including paved and unpaved roads, was 0.73 km/km². Topography was flat to moderately rolling with 0–30° slope. Landforms of this region have been described by Prior (1991) and vegetation associations have been described by Kane et al. (2002).

METHODS

We captured bobcats using baited box traps (Model no. TLT 209.5, Tomahawk Co., Tomahawk, WI) or foothold traps (No. 3 Victor Softcatch®, Woodstream Corp., Lititz, PA). Additionally, we marked bobcats that were incidentally live-captured by licensed private trappers if they were uninjured and fell within the study area. We anesthetized bobcats via an intramuscular injection of ketamine HCl and xylazine HCl (5:1, 10 mg/kg). We ear-tagged each individual and estimated age based on weight and tooth condition. Age estimates consisted of 3 categories: 1) kitten, weighing <3.5 kg and milk teeth present; 2) juvenile, weighing between 3.5 kg and 5.5 kg and no tooth wear visible; and 3) adult, weighing ≥5.5 kg and some tooth wear present. We extracted an upper lateral incisor from adult bobcats and sent it to Matson’s Laboratory (Milltown, MT)

for a more exact determination of age via cementum analysis (Crowe 1972).

We fitted juvenile bobcats with standard very high frequency (VHF) radiocollars (145–160 g, Advanced Telemetry Systems, Isanti, MN; 170 g, Lotek Wireless, Newmarket, ON) equipped with a foam insert to allow for growth. We fitted adult bobcats with either a standard VHF radiocollar or a Global Positioning System (GPS) collar (350 g, Advanced Telemetry Systems; 292 g, Lotek Wireless). In all cases, we ensured that the radiocollar weighed $\leq 5\%$ of the animal's body weight. The GPS radiocollars were also equipped with drop-off mechanisms to allow for data recovery. We conducted capture and handling procedures in accordance with Iowa State University Institutional Animal Care and Use Committee protocol (5-03-5447-W).

We conducted radiotelemetry using vehicle mounted yagi antennas arrayed in a null-peak configuration (Samuel and Fuller 1996). We used Location of a Signal (LOAS) 3.0.4 software (Ecological Software Solutions™, Sacramento, CA) and a GPS to triangulate bobcat locations. We determined the locations using ≥ 2 bearings taken ≤ 15 minutes of one another. Generally, we collected only 2 bearings in instances where the bobcat was in a low spot (e.g., stream bed) and the technician could only hear the signal from 2 locations. We used the maximum likelihood algorithm in LOAS to calculate telemetry error for bobcat locations with ≥ 3 bearings, which produced error ellipses from triangulation based on the multiple azimuths (Millspaugh and Marzluff 2001). We used test collars at known locations to determine accuracy and precision of our radiotelemetry methods (White and Garrott 1990, Millspaugh and Marzluff 2001).

We located each bobcat 1–2 times per week (hereafter, point locations). In addition to point locations, we sequentially tracked a sample of adult females 16 weeks each year during April–September. We tracked these females for a 6-hour sampling period once a week. During the sampling period, we located each female every 15–30 minutes (hereafter, sequential locations). We rotated tracking schedules every week so that we collected point and sequential locations throughout the entire diel period, which takes into account habitats used for both resting and foraging and other active behaviors. At the time of location, we recorded the bobcat as either active or resting depending on the variability in the radio signal (Kenward 1987). We located GPS-collared bobcats on the same schedule as VHF-collared bobcats. Upon recovery of a GPS collar, we downloaded stored data and combined it with triangulated locations.

We used SAS 9.1 software (SAS Institute Inc., Cary, NC) to create a data set for each bobcat including all point locations, one randomly selected sequential location from each sampling period, and the 3-dimensional locations from recovered GPS collars. We used only 3-dimensional locations from GPS collars that were typically accurate to ≤ 100 m (Gosselink and Clark 2004). We removed any locations that were < 24 hours apart to increase independ-

ence between locations (White and Garrott 1990). We examined statistical distribution of location error ellipses and removed locations in the upper 10% (> 13.48 ha; White and Garrott 1990). We examined all data sets for errors and inconsistencies such as incorrect data entry, insufficient amounts of information, and proper time succession. We split location data into 2 seasons: 1) 1 April–30 September and 2) 1 October–31 March, based on changes in female behavior during the denning and kitten-rearing times of year (Bailey 1974, Lovallo and Anderson 1996, Chamberlain et al. 2003).

We calculated home ranges and cores of adult resident bobcats using a fixed kernel estimator with least squares cross validation (Worton 1989, Seaman and Powell 1996) in the Animal Movement extension (Hooge and Eichenlaub 1997) for ArcView. We used a 95% utilization distribution (UD) to calculate home range areas and a 50% UD to calculate core areas (Powell 2000). To determine adequate sample size we focused on suggestions by Seaman et al. (1999) that kernel home range estimates for carnivores like bobcats tend to stabilize at about 30 locations. We examined the sampling distribution of UD's by randomly selecting 15–50 locations from each bobcat data set at intervals of 5, and then we calculated a home range from those randomly selected locations (Seaman et al. 1999). We used analysis of variance procedures (SAS Institute Inc.) to examine the change in home range area as a function of number of locations used to calculate the home range. We considered a bobcat a resident if it had not made a permanent one-way movement outside the boundary of the natal or previously established home range (Kamler and Gipson 2000). We transformed all UD's logarithmically to approximate a normal distribution (Ramsey and Schafer 2002). We used a mixed model procedure (SAS Institute Inc.), which accounts for multiple observations on the same individual, to test for differences in home range and core area between sexes, ages, seasons, and years.

We examined habitat selection at 2 orders (Johnson 1980) using 3 methods of analysis, similar to the approach taken by Chamberlain et al. (2003). First, we compared the habitat composition of home ranges to that of the study area (Second order), the habitat composition of cores to that of home ranges (Third order), and the habitat composition of where bobcats were located compared with the habitat within their home ranges (Third order). To accomplish this latter analysis, we estimated habitat use by buffering each bobcat location with an area equivalent to the median error ellipse of our study (3.65 ha) for all locations, and calculated the habitat composition within these buffers (Gosselink et al. 2003).

We used the Iowa DNR, Geological Survey 2002 Land Cover raster data set, which was created using Landsat satellite imagery with a spatial resolution of 15 m. We collapsed the original 17 land covers into 9 habitat classes that we determined would be functionally important for bobcats: 1) Water–Wetland, 2) Forest, 3) Grassland, 4) CRP, 5) Row crop, 6) Road, 7) Residential–Industrial, 8) Barren, and 9) Unclassified (Koehler 2006).

Table 1. Statistics of the habitat variables used to predict size and shape of home ranges and size of bobcat cores in south-central Iowa, USA, 2003–2006. We calculated statistics from 119 seasonal home ranges and cores.

Model	Dependent variable	Independent variables	Units	\bar{x}	SD	
Home range	Area	Patch density	no./100 ha	68.34	12.06	
	Area, shape	Patch size SD	ha	16.80	9.52	
	Area, shape	Presence-absence of paved roads		0.11	0.18	
	Area, shape	Stream density	km/km ²	1.73	0.52	
	Shape	Mean slope	degrees	4.41	0.69	
	Area	CRP largest patch index ^a	%	1.87	1.58	
	Shape	CRP patch size SD	ha	3.49	1.88	
	Shape	Mean distance between CRP patches	m/ha	65.32	10.67	
	Area	Forest largest patch index ^a	%	8.29	6.66	
	Shape	Forest patch density	no./100 ha	9.91	1.72	
	Area, shape	Forest edge density	m/ha	76.40	17.07	
	Area	Forest patch size SD	ha	18.13	13.09	
	Area	Mean grassland patch size	ha	2.77	1.15	
	Shape	Mean distance between grassland patches	m	41.26	2.66	
	Shape	Grassland interspersions-juxtaposition index ^a	%	75.14	4.80	
	Area	Row crop largest patch index ^a	%	2.58	1.97	
	Area	Row crop patch size SD	ha	9.35	5.93	
	Shape	Mean distance between row crop patches	m	79.05	31.63	
	Area	Row crop interspersions-juxtaposition index ^b	%	29.16	5.12	
	Shape	Row crop aggregation index ^c	%	88.76	2.40	
	Core	Area	Largest patch index ^a	%	29.43	14.93
		Area	Patch size SD	ha	8.38	4.14
		Area	Presence-absence of paved roads	km/km ²	0.08	0.34
Area		Stream density	km/km ²	2.90	1.79	
Area		CRP largest patch index ^a	%	4.52	5.48	
Area		CRP patch size SD	ha	2.21	1.94	
Area		Forest largest patch index ^a	%	19.77	15.91	
Area		Mean forest patch size	ha	3.89	4.68	
Area		Proportion grassland	%	37.71	10.63	
Area		Grassland patch density	no./100 ha	20.57	8.03	
Area		Grassland interspersions/juxtaposition index ^b	%	71.35	8.29	
Area		Row crop patch size SD	ha	4.53	4.05	

^a % of the total landscape area comprised by the largest patch. CRP, Conservation Reserve Program.

^b % of patch intermixing with other habitat classes.

^c % of patch aggregation for the specified habitat class.

We used compositional analysis to determine sex-specific habitat selection (Aitchison 1982, Aebischer et al. 1993). We removed the Unclassified habitat class from the analysis because it was not present in any of the home ranges and we used Barren as the reference habitat class. We used multivariate analysis of variance (MANOVA) procedures (SAS Institute Inc.) to test for differences between the log-ratios of used and available habitats. If MANOVA results indicated significant selection, we used *t*-tests ($\alpha = 0.05$) to determine if there was a difference between pairs of habitat classes and to create rank matrices (Aebischer et al. 1993). For both the MANOVA and *t*-tests, we weighted the log-ratios by the square root of the number of locations for each animal (Phillips et al. 2003). We also calculated standardized selection ratios using the geometric mean for each habitat class to determine magnitude of selection (Pendleton et al. 1998, Phillips et al. 2003). We demonstrated the relative strength of selection among habitat classes using the inverse of the number of resources available (0.125; Krebs 1999).

We used multiple linear regression, with a mixed model error structure (SAS Institute Inc.) to account for multiple observations on the same individual, in modeling the home range and core area as a function of composition, class, and landscape habitat variables (Manly et al. 2002). Based on

literature and our hypotheses about bobcat landscape ecology, we initially chose 48 composition and configuration variables that could be calculated at the home range and core scales. We calculated the composition variables from Geographic Information System (GIS) layers created by the Iowa DNR, Geological Survey, which included variables such as stream and road density. We used FRAGSTATS 3.3 (McGarigal and Marks 1995) to calculate class and landscape variables. Class variables are measurements pertaining to a specific habitat class such as Forest patch density. We classified landscape variables across the entire landscape mosaic and included measurements such as patch density, regardless of habitat class. We checked these variables for normality and transformed nonnormal variables logarithmically (Ramsey and Schafer 2002). For all logarithmically transformed variables, the data appeared closer to meeting the assumption of normality after transformation. We designated composition variables with $\geq 40\%$ of missing values as either present or absent. We first reduced the number of potential predictor variables by removing one variable from each pair of correlated variables with a Pearson's correlation coefficient of ≥ 0.70 . We removed the variable in the pair that was correlated with the highest number of other variables first, and in the case of

Table 2. Mean home range (HR; 95% utilization distribution [UD]) and core (50% UD) area (km²) of 47 resident bobcats in south-central Iowa, USA, during 2003–2006.

Season	Sex	Individuals	UDs ^a	Relocations		HR size		Core size	
				\bar{x}	Range	\bar{x}	95% CI	\bar{x}	95% CI
1 Apr–30 Sep	F	23	41	43	25–64	16.8	13.7–20.7	1.8	1.4–2.3
	M	21	26	38	20–52	56.9	41.0–71.9	7.3	5.4–9.7
1 Oct–31 Mar	F	15	31	38	26–51	24.1	19.0–30.7	2.8	2.2–3.7
	M	17	21	32	20–66	59.3	45.7–76.9	8.0	5.8–11.0

^a We calculated some UD's on the same individual in multiple years.

equal numbers of cross-correlations, we removed the variable with the lowest correlation to the dependent variable. We further accounted for the partial correlation structure using R-square model selection (SAS Institute Inc.) to reduce the model set. This process led us to consider models with as many as 12 variables with the highest correlation to the dependent variables (Table 1) and a final set of about 15 ecologically understandable potential home range and core area models to compare. We considered only linear models of these variables without interaction because we wanted to focus on the relative importance of variables and to avoid constructing more model combinations than we could resolve with the data.

We compared the best-fit candidate models, based on multiple regression using Akaike's Information Criterion, corrected for small sample size (AIC_c; Burnham and Anderson 2002). We included sex as a main effect in all models because of the significant difference in area between UD's for females and males and repeated the process with both sex and number of UD polygons included into the model because of the effect of the number polygons on perimeter to area ratios. We created models using the seasonal home ranges, although we did not allow seasons to vary within the models because we wanted the models to be easily applied to real world situations. We ranked candidate models using ΔAIC_c values and assessed the relative likelihood of each model using Akaike weights (w_i ; Burnham and Anderson 2002).

In addition to creating predictor models of area, we used the habitat variables to create predictive functions of home range shape. We calculated a shape index (S) defined as

$$S = p / (2\sqrt{A \times \pi})$$

where p is the perimeter of the home range and A is the home range area (Forman and Godron 1986). Shape index is an index of how much more home range perimeter there is compared to a circle with the same area. A shape index of 1.00 indicates a circular home range.

We used the same procedures as described above to reduce the original set of 48 predictor habitat variables to 12 (Table 1). We included the number of home range polygons into all models to account for its effect on shape index because shape index is directly related to the amount of perimeter, and we repeated the process with both sex and the number of UD polygons included into each model.

RESULTS

We radiocollared 68 (29 F, 39 M) bobcats from 3 March 2003 to 27 March 2006 (52 VHF collars, 16 GPS collars). We collected 12,966 locations and recovered an additional 1,399 3-dimensional locations from 7 GPS collars. Of the locations we collected, 6,840 were point locations and 6,171 were sequential locations. Also, 91.5% of our locations were based on ≥ 3 bearings that had estimated errors, 4.5% were visuals or homing locations of bobcats with little to no error, and 5.0% were based on 2 bearings with no error estimation. We collected 45% of locations from 0800 hours to 2000 hours (i.e. daytime) and 55% from 2000 hours to 0800 hours (i.e. nighttime). The proportion of active locations (51–63%) exceeded that of resting locations during 0700–0800 hours and 1700–2200 hours, indicating a crepuscular activity pattern. Our radiotelemetry tests using reference collars revealed a standard deviation of 5.20 and a bias of 1.19 degrees (Gosselink and Clark 2005). We experienced 8 GPS collar failures (2 F, 6 M). We recovered 2 of the failed GPS collars (1 F, 1 M) at later dates and used location data stored on them for analyses.

We used 5,261 locations to calculate 119 estimates of seasonal home ranges and cores from multiple observations on 47 resident bobcats (23 F, 24 M). Although our sampling distribution suggested that ≥ 25 and 20 locations per season was sufficient for calculating UD's for females and males, respectively, we far exceeded this standard with an average of 41 (range = 25–64) and 36 (range = 20–66) locations per UD for females and males, respectively (Koehler 2006). The UD's of male bobcats in the October–March season was our smallest sample, and the median number of locations of this group was 28 with most UD's estimated from ≥ 32 locations. There was no difference in home range area among years ($F_{3,16} = 0.22$, $P = 0.88$) or annual age classes ($F_{5,21} = 1.45$, $P = 0.25$). Home range area of males was nearly 3 times that of females ($F_{1,43} = 85.62$, $P < 0.001$; Table 2). Home range area of females was 30% smaller in April–September as compared to October–March ($t_{16} = -2.31$, $P = 0.03$; Table 2), whereas males did not differ between seasons ($t_{43} = -0.24$, $P = 0.8140$; Table 2).

Similarly, there was no difference in core area among years ($F_{3,16} = 0.34$, $P = 0.80$) or annual age classes ($F_{5,21} = 0.68$, $P = 0.65$). Core area differed between sexes ($F_{1,43} = 77.59$, $P < 0.001$), with males maintaining larger core areas than females (Table 2). Only females had significantly smaller

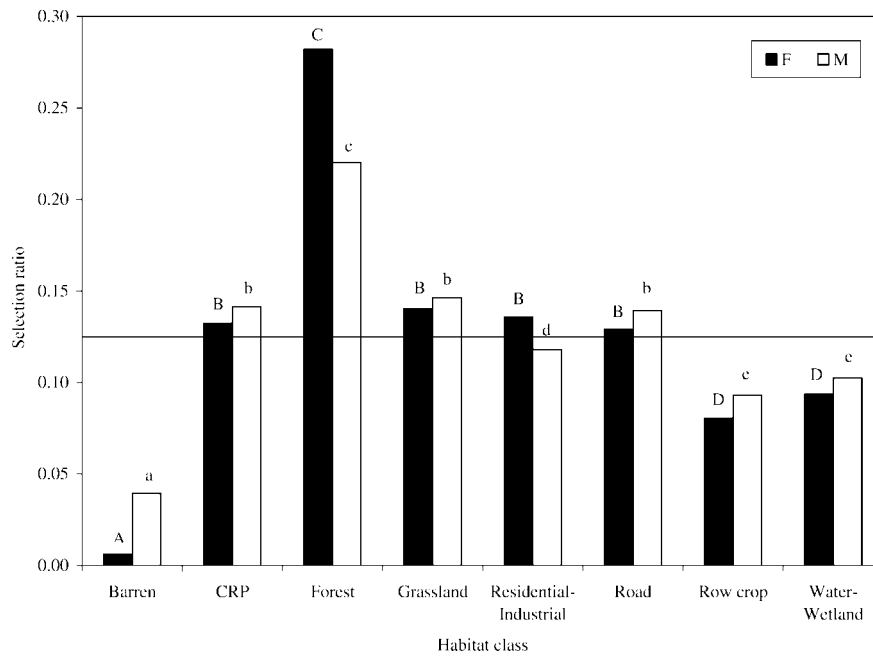


Figure 2. Standardized habitat selection ratios of female and male bobcats at the home range (used) versus study area (available) scale in south-central Iowa, USA, 2003–2006. The horizontal line indicates random selection (Krebs 1999). Habitat classes with significantly different selection ratios are indicated by different letters for females (uppercase) and males (lowercase).

core areas in April–September as compared to October–March ($t_{16} = -2.45$, $P = 0.02$; Table 2).

We determined the differences in log-ratios of used versus available habitat for all bobcats were significant for all 3 methods of analysis (Wilk's $\Lambda < 0.001$), as were the differences for females and males separately. As expected, Forest ranked as the most important habitat class for females and males for all 3 methods of analysis. In most cases, Grassland and CRP ranked

as the second and third most important habitat classes. However, t -tests revealed that Grassland was only selected at a significantly higher magnitude than CRP when comparing the habitat selected at bobcat locations to that available in the home range (Figs. 2–4).

Standardized selection ratios revealed that Forest was selected for twice as often as random selection would have predicted for both females and males for all 3 methods of

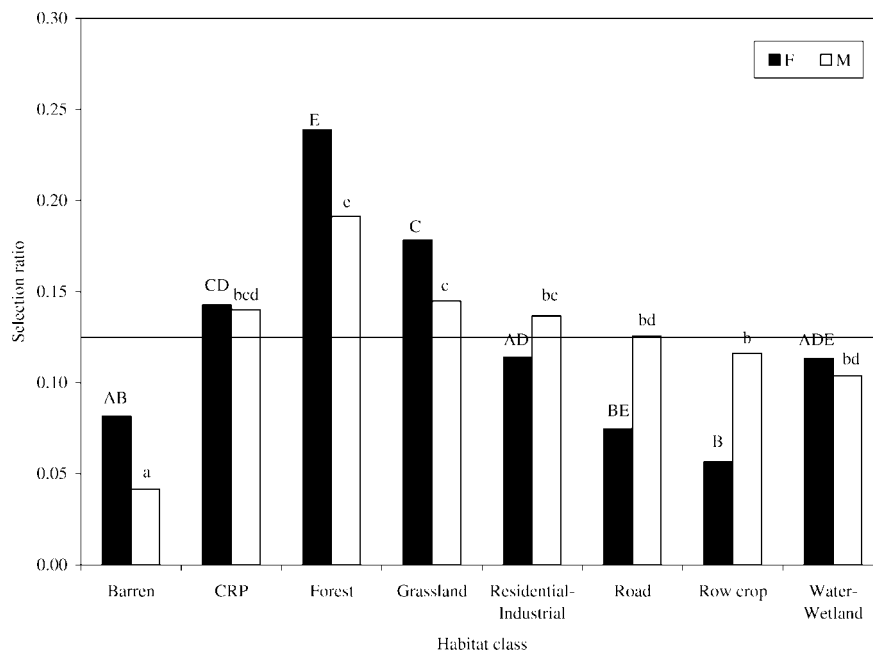


Figure 3. Standardized habitat selection ratios of female and male bobcats at the core (used) versus home range (available) scale in south-central Iowa, USA, 2003–2006. The horizontal line indicates random selection (Krebs 1999). Habitat classes with significantly different selection ratios are indicated by different letters for females (uppercase) and males (lowercase).

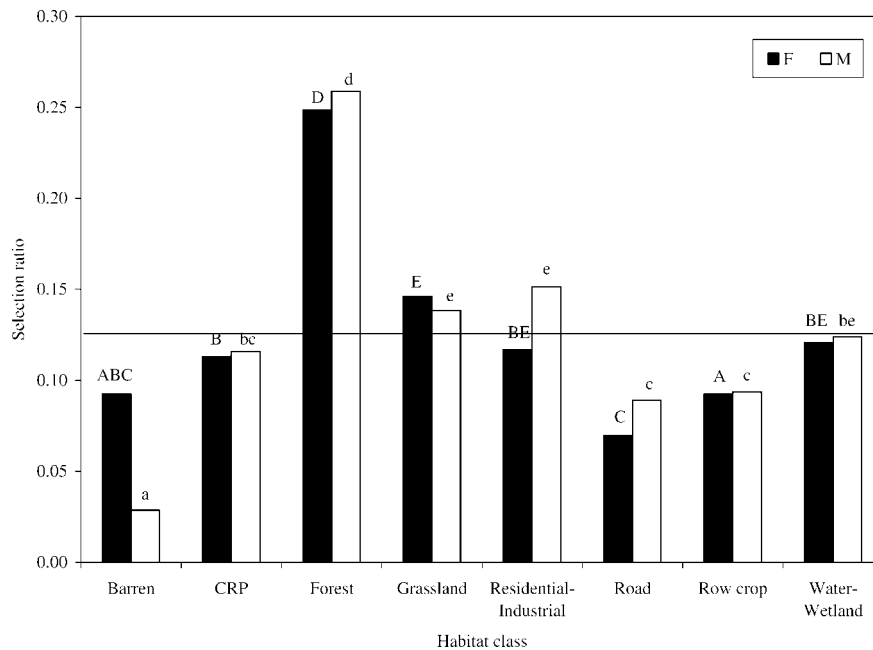


Figure 4. Standardized habitat selection ratios of female and male bobcats at the point locations (used) versus home range (available) scale in south-central Iowa, USA, 2003–2006. The horizontal line indicates random selection (Krebs 1999). Habitat classes with significantly different selection ratios are indicated by different letters for females (uppercase) and males (lowercase).

analysis (Figs. 2–4). Females selected Forest 2.0, 1.3, and 1.7 times more often than Grassland when comparing the habitat used within the home range to that available within the study area, the habitat used within the core to that available within the home range, and the habitat used where bobcats were located to that available within the home range, respectively. Similarly, males selected Forest 1.5, 1.3, and 1.9 times more often than Grassland when comparing the habitat used within the home range to that available within the study area, the habitat used within core to that available within the home range, and the habitat used where bobcats were located to that available within the home range, respectively. In most cases, selection of Grassland and CRP did not appear to differ from random, except perhaps when comparing female and male core use to home range availability (Fig. 3). The selection ratio for the Row crop habitat class was less than random for both females and males for all 3 methods of analysis.

Results of our modeling exercise indicated that there were 3 competing models (i.e., $\Delta AIC_c < 2$) for home range area, all of which included nearly the same parameters (Table 3). The overall best-fit home range area model ($R^2 = 0.86$) included 5 habitat variables (Table 3). Parameter estimates indicate that as stream density and percentage of the home range comprised of a single CRP or Row crop patch increased, home range area decreased (Table 4). Furthermore, as variability in area among all patches and row crop patches decreased, home range area decreased (Table 4). Including number of home range polygons did not improve model fit ($\Delta AIC_c = 7.3$).

There were 4 competing habitat models for predicting core area, all of which included similar parameters (Table 5). We report the core area model with $\Delta AIC_c = 0.0$ ($R^2 = 0.89$),

which included 4 habitat variables in addition to a variable for sex (Table 5). As variability in area among all patches decreased, core area decreased. As stream density and percentage of the home range comprised of a single patch increased, core area decreased (Table 6). Furthermore, when paved roads were absent, core area decreased (Table 6). Grassland (48%) and Forest (44%) habitat classes comprised the largest single patch in most cores. The best-fit model did not include number of core area polygons as a variable (Table 5).

Table 3. Akaike's Information Criterion corrected for small sample sizes (AIC_c), ΔAIC_c , and model weights of the 3 best-fit regression models for predicting the area of bobcat home ranges in south-central Iowa, USA, during 2003–2006. We included sex a priori as a main effect.

Model	No. parameters	Parameters	AIC_c	ΔAIC_c
1	6	Sex Patch size SD Stream density CRP largest patch index ^a Row crop largest patch index Row crop patch size SD	82.1	0.0
2	5	Sex Patch size SD Stream density Row crop largest patch index Row crop patch size SD	83.1	1.9
3	6	Sex Patch size SD Forest largest patch index Forest patch size SD Row crop largest patch index Row crop patch size SD	84.6	3.4

^a CRP, Conservation Reserve Program.

Table 4. Parameter estimates of the best-fit regression model for predicting the size of bobcat home ranges in south-central Iowa, USA, during 2003–2006. We included sex a priori as a main effect.

Model parameters	β	SE	<i>t</i>	<i>P</i>
Intercept	2.989	0.167	17.85	<0.001
Sex	0.377	0.080	4.73	<0.001
Patch size SD	0.029	0.004	7.13	<0.001
Stream density	-0.243	0.064	-3.79	<0.001
CRP largest patch index ^a	-0.114	0.045	-2.52	0.016
Row crop largest patch index	-0.140	0.023	-6.09	<0.001
Row crop patch size SD	0.064	0.008	8.11	<0.001

^a CRP, Conservation Reserve Program.

Home range shape indexes ranged from 1.27 to 3.37. Results showed that there were 4 competing models (Table 7). In addition to variables that were included as main effects (i.e., no. of home range polygons and sex), the best-fit home range shape model ($R^2 = 0.62$) included 2 habitat variables (Table 7). As the aggregation of Row crop patches increased, home range shape index decreased (Table 8). And, as density of unpaved roads decreased, home range shape index decreased (Table 8). Our best-fit model included sex, although 3 of the 5 competing models did not, indicating ultimately that sex may not be important predictor of home range shape (Table 7).

DISCUSSION

Due to the fragmented landscape in southern Iowa, we hypothesized that bobcats would maintain larger home range areas than those reported elsewhere. However, our results indicated bobcats are using similar amounts of area to those reported from elsewhere in the species range (ID, Bailey 1974; MO, Hamilton 1982; WI, Lovallo and Anderson 1996; AR, Rucker et al. 1989), but somewhat larger than those

Table 5. Akaike's Information Criterion corrected for small sample sizes (AIC_c), ΔAIC_c , and model weights of the 4 best-fit regression models for predicting the area of bobcat cores in south-central Iowa, USA, during 2003–2006. We included sex and number of polygons a priori as main effects.

Model	No. parameters	Parameters	AIC_c	ΔAIC_c
1	5	Sex Largest patch index Patch size SD Presence-absence of paved roads Stream density	104.1	0.0
2	5	Sex No. of polygons Largest patch index Patch size SD Stream density	104.5	0.4
3	6	Sex No. of polygons Largest patch index Patch size SD Presence-absence of paved roads Stream density	104.5	0.4
4	4	Sex Largest patch index Patch size SD Stream density	105.1	1.0

Table 6. Parameter estimates of the best-fit regression model for predicting the area of bobcat cores in south-central Iowa, USA, during 2003–2006. We included sex and number of polygons a priori as main effects.

Model parameter	β	SE	<i>t</i>	<i>P</i>
Intercept	0.987	0.131	7.52	<0.001
Sex	0.426	0.075	5.68	<0.001
Largest patch index	-0.036	0.002	-15.38	<0.001
Patch size SD	0.155	0.009	16.96	<0.001
Presence-absence of paved roads	0.187	0.092	2.04	0.048
Stream density	-0.049	0.019	-2.51	0.016

reported from Oklahoma (Rolley 1983), Kansas (Kamler and Gipson 2000), and Illinois (Nielsen and Woolf 2001). However, smaller home range estimates are commonly reported from the southeastern (LA, Hall and Newsom 1976; SC, Buie et al. 1979; AL, Miller and Speake 1979; FL, Maehr 1997; MS, Chamberlain et al. 2003; GA, Diefenbach et al. 2006) and southwestern (CA, Riley et al. 2002) United States, and therefore our estimates of home range size are among the largest reported for the species.

If we assume exclusive home ranges of adult female bobcats and habitat saturation we can calculate a rudimentary estimate of density from the average home range (Lembeck and Gould 1979). Our minimum estimated density of 10 bobcats/100 km² is similar to that reported from nearby Missouri and Minnesota (Anderson and Lovallo 2003).

We found bobcats selecting Forest above all other habitat classes, and when we located radiocollared bobcats, we consistently found them in habitat with brushy, dense understory where desirable prey and escape cover were evident (Anderson and Lovallo 2003). Selection for forest habitat was especially evident when we compared habitat selected at bobcat locations with that available in the home ranges. Bobcats used row crop agriculture infrequently, which we interpreted as avoidance by bobcats. On average, the largest Row crop patch within any home range comprised of <3% of the entire home range. Similarly, Nielsen and Woolf (2002) studied bobcat habitat-abundance relationships in southern Illinois and found that

Table 7. Akaike's Information Criterion corrected for small sample sizes (AIC_c), ΔAIC_c , and model weights of the 4 best-fit regression models for predicting the shape index of bobcat home ranges in south-central Iowa, USA, during 2003–2006. We included sex and number of polygons a priori as main effects.

Model	No. parameters	Parameters	AIC_c	ΔAIC_c
1	4	No. of polygons Sex Unpaved road density Row crop aggregation index	-1.9	0.0
2	3	No. of polygons Unpaved road density Row crop aggregation index	-1.4	0.5
3	2	No. of polygons Row crop aggregation index	-0.9	1.0
4	3	No. of polygons Patch size SD Row crop aggregation index	0.0	1.9

Table 8. Parameter estimates of the best-fit regression model for predicting the shape index of bobcat home ranges in south-central Iowa, USA, during 2003–2006. We included sex and number of polygons a priori as main effects.

Model parameter	β	SE	t	P
Intercept	3.951	0.769	5.14	<0.001
No. of polygons	0.223	0.019	11.99	<0.001
Sex	-0.098	0.043	-2.28	0.028
Unpaved road density	0.123	0.057	2.17	0.036
Row crop aggregation index	-0.027	0.009	-3.19	0.003

bobcats selected forest habitat, and population abundance was negatively correlated with row crop agriculture.

Although bobcats selected forest habitat the most, our data also indicated that bobcats selected for forest patches surrounded by grasslands and CRP within their intensive use areas (i.e., cores). In 65% of bobcat home ranges and in 48% of cores, grasslands comprised the largest single patch of habitat, compared with forests comprising the largest single patch of habitat in 29% of bobcat home ranges and in 44% of cores. Grassland and CRP were selected more than random use for all 3 methods of analysis. But, when we compared the habitat selected where we located bobcats to that available in the home range, selection for Grassland and CRP was not different from random. Our interpretation of this hierarchical habitat selection pattern is that although forest habitat appears to be the most important landscape component to bobcats in Iowa (i.e., Second order selection), perennial grassland and CRP are important for the way in which they contribute to the context of the landscapes selected by bobcats (i.e., Third order selection; Johnson 1980). Although we expected more use of CRP, especially for hunting forays, this was not evident in our data. Our results do not support the hypothesis that presence of CRP during the past 20 years was an important factor in the recolonization of bobcats in Iowa.

In more fragmented landscapes bobcats used larger home range and core areas, and in less fragmented landscapes bobcats used smaller home range and core areas. In all modeling exercises, as variability in patch size increased the amount of home range and core areas used also increased. Variability in patch size among all patches regardless of habitat class, as well as variability in patch size within a specific habitat class, was highly correlated with home range and core area. We confirmed the importance of variability of Forest and Grassland patch size by removing the general patch size standard deviation variable from our models (Tables 4, 6) to see which other variables would replace it during model selection. From this exercise, we discovered that the standard deviation of Forest and Grassland patch size replaced the general patch size variable in the best-fit models. In Iowa, like many parts of the agricultural Midwest, much of the forested habitat is associated with rivers and streams (Widner 1968), which is consistent with our observation that stream density was also a significant predictor variable in the home range and core area models. Other factors that may be affecting the amount of area used that we did not incorporate into our models are food availability, social structure,

adjacencies between individuals, population density, and location on the landscape (Powell 2000).

Our home range and core area modeling suggests that the configuration of forest and perennial grassland may ultimately affect not only the density of bobcats but also their distribution on the landscape. Researchers express varying degrees of the importance of territoriality among bobcats but typically exhibit relatively little intrasexual overlap of home ranges or cores (Kitchings and Story 1979, Anderson 1987, Lovallo and Anderson 1996, Nielsen and Woolf 2001, Diefenbach et al. 2006). Therefore, as fragmentation increases and the amount of area used by bobcats increases, it is reasonable to assume that density of bobcats will decrease. Although we do not necessarily expect this decrease to be a linear change because it will also be a function of the specific landscape configuration, social interactions, prey availability, and other factors, it is certainly reasonable to expect that bobcats will be less dense in much of the intensively farmed areas of the Midwest. Our prediction is consistent with results of Crooks (2002), who determined that as fragmentation increased, abundance and probability of occurrence of bobcats decreased.

Although the determination of home range boundaries is difficult to establish with certainty, we calculated an index to shape so that we might understand how landscape characteristics guided home range establishment (Powell 2000). We initially thought home range boundaries would be linear because bobcats may be placing their home ranges along streams and rivers, but the result from our home range shape model did not support this hypothesis. Home ranges were more circular in landscapes where row crop fields were smaller and dispersed among forest and grassland habitat patches (i.e., a low degree of Row crop aggregation index). In contrast bobcats exhibited home ranges that were more irregular in shape where row crop fields were larger and comprised a larger proportion of the home range (i.e., a high degree of Row crop patch aggregation). Results of our shape modeling, coupled with our habitat selection analysis, support the conclusion that bobcats avoid areas with large proportion of row crop agriculture, which might be especially obvious in the nongrowing season when Row crop patches would be barren.

In summary, our results stress the importance of forest habitat for bobcats, especially in agricultural landscapes. Although the proportion of forest habitat available is important, configuration of this and associated habitats appears important in determining the amount of area used and thus the potential density of bobcats on the landscape. We derived our models from data within the relatively diverse landscape of southern Iowa. It remains to be seen if our models will be useful predictors of habitat use and potential density in other areas of Iowa where row crops are even more dominant on the landscape and interspersed grassland habitats are lacking.

Beneficial future research could incorporate these habitat selection patterns into a model of continuing expansion of bobcats into other areas of Iowa and the Midwest. An

important component of such research would be an understanding of how these types of landscape affect bobcat dispersal and movements.

MANAGEMENT IMPLICATIONS

Our analyses from the southern part of the Corn Belt of the Midwest confirm the importance of forest as a primary habitat feature selected by bobcats. But our results emphasize that bobcats selected landscapes where forest patches were surrounded by perennial grassland, as opposed to forest patches surrounded only by annual row crops. Furthermore, as patch size became more variable, home range size and shape became larger and more variable, leading to the prediction that bobcats will be more sparsely distributed on this agricultural landscape than in other areas of the species range. In Iowa, the fragmented landscape is also associated with relatively uniform human density that also exposes bobcats to anthropogenic hazards including trapping and automobile collision, thereby reducing survival. Population managers will need to carefully account for the more fragmented distribution of preferred landscape elements, lower density, and potentially slower spread of bobcats into the center of the Corn Belt as compared to other areas in the species range where land use is less intensive.

ACKNOWLEDGMENTS

Funding for our research was provided by the Iowa DNR and State Wildlife Grants. We would like to thank J. Coffey, M. Purvis, C. Duncan, N. McCann, B. Orning-Tschampl, J. Bolis, H. Stricker, C. Tucker, M. Jones, S. Hansen, J. Kanine, and S. Williams for countless hours of field work. R. McNeely, J. D. Davis, and J. Parkhurst provided GIS assistance. In addition, our research was made possible by many trappers who assisted in capturing bobcats.

LITERATURE CITED

- Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74: 1313–1325.
- Aitchison, J. 1982. The statistical analysis of compositional data. *Journal of the Royal Statistical Society* 44:139–177.
- Anderson, E. M. 1987. A critical review and annotated bibliography of literature on the bobcat. Colorado Division of Wildlife Special Report 62. Colorado Department of Natural Resources, Denver, USA.
- Anderson, E. M., and M. J. Lovallo. 2003. Bobcat and lynx. Pages 758–786 in G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. *Wild mammals of North America*. John Hopkins University Press, Baltimore, Maryland, USA.
- Bailey, T. N. 1974. Social organization in a bobcat population. *Journal of Wildlife Management* 38:435–446.
- Buie, D. E., T. T. Fendley, and H. McNab. 1979. Fall and winter home ranges of adult bobcats on the Savannah River Plant. Pages 42–46 in L. G. Blum and P. C. Escherich, editors. *Bobcat research conference proceedings*. National Wildlife Federation Scientific and Technical Series 6, Front Royal, Virginia, USA.
- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference*. Second edition. Springer-Verlag, New York, New York, USA.
- Chamberlain, M. J., B. D. Leopold, and L. M. Conner. 2003. Space use, movements and habitat selection of adult bobcats (*Lynx rufus*) in Central Mississippi. *American Midland Naturalist* 149:395–405.
- Crooks, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. *Conservation Biology* 16:488–502.
- Crowe, D. M. 1972. The presence of annuli in bobcat tooth cementum layers. *Journal of Wildlife Management* 36:1330–1332.
- Deems, E. F., Jr., and D. Pursley. 1978. North American furbearers, their management, research and harvest status in 1976. Association of Fish and Wildlife Agencies, Washington, D.C., USA.
- Diefenbach, D. R., L. A. Hansen, R. J. Warren, and M. J. Conroy. 2006. Spatial organization of a reintroduced population of bobcats. *Journal of Mammalogy* 87:394–401.
- Dinsmore, J. J. 1994. *A country so full of game: the story of wildlife in Iowa*. University of Iowa Press, Iowa City, USA.
- Forman, R. T. T., and M. Godron. 1986. *Landscape ecology*. John Wiley and Sons, New York, New York, USA.
- Frey, S. N., and M. R. Conover. 2006. Habitat use by meso-predators in a corridor environment. *Journal of Wildlife Management* 70:1111–1118.
- Gosselink, T. E., and W. R. Clark. 2004. Distribution and population dynamics of bobcats in Iowa. State Wildlife Grant Report T-1-R-5, Iowa Department of Natural Resources, Des Moines, USA.
- Gosselink, T. E., and W. R. Clark. 2005. Distribution and population dynamics of bobcats in Iowa. State Wildlife Grant Report T-1-R-5, Iowa Department of Natural Resources, Des Moines, USA.
- Gosselink, T. E., T. R. Van Deelen, R. E. Warner, and M. G. Joselyn. 2003. Temporal habitat partitioning and spatial use of coyotes and red foxes in east-central Illinois. *Journal of Wildlife Management* 67:90–103.
- Hall, H.T., and J. D. Newsom. 1976. Summer home ranges and movement of bobcats in bottomland hardwoods of southern Louisiana. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 30:422–436.
- Hamilton, D. A. 1982. *Ecology of the bobcat in Missouri*. Thesis, University of Missouri, Columbia, USA.
- Hooge, P. N., and B. Eichenlaub. 1997. *Animal movement extension to ArcView*. Version 1.1. Alaska Science Center, Biological Science Office, U.S. Geological Survey, Anchorage, Alaska, USA.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- Kamler, J. F., and P. S. Gipson. 2000. Home range, habitat selection, and survival of bobcats, *Lynx rufus*, in a prairie ecosystem in Kansas. *Canadian Field-Naturalist* 114:388–394.
- Kane, K. L., E. E. Klaas, K. L. Andersen, P. Brown, and R. L. McNeely. 2002. The Iowa Gap Analysis Project Final Report. Iowa Cooperative Fish and Wildlife Research Unit, Iowa State University, Ames, USA.
- Kenward, R. 1987. *Wildlife radio tagging*. Academic Press, London, United Kingdom.
- Kitchings, J. T., and J. S. Story. 1979. Home range and diet of bobcats in eastern Tennessee. Pages 47–52 in L. G. Blum and P. C. Escherich, editors. *Bobcat research conference proceedings*. National Wildlife Federation Scientific and Technical Series 6, Front Royal, Virginia, USA.
- Koehler, S. A. 2006. *Habitat selection and demography of bobcats (Lynx rufus) in Iowa*. Thesis, Iowa State University, Ames, USA.
- Krebs, C. J. 1999. *Ecological methodology*. Second edition. Addison-Wesley, Menlo Park, California, USA.
- Lembeck, M., and G. I. Gould, Jr. 1979. Dynamics of harvested and unharvested bobcat population in California. Pages 53–54 in L. G. Blum and P. C. Escherich, editors. *Bobcat research conference proceedings*. National Wildlife Federation Scientific and Technical Series 6, Front Royal, Virginia, USA.
- Lovallo, M. J., and E. M. Anderson. 1996. Bobcat (*Lynx rufus*) home range size and habitat use in northwest Wisconsin. *American Midland Naturalist* 135:241–252.
- Machr, D. S. 1997. The comparative ecology of bobcat, black bear, and Florida panther in south Florida. *Bulletin of the Florida Museum of Natural History* 40:1–176.
- Machr, D. S., R. F. Noss, and J. F. Larkin. 2001. *Large mammal restoration*. Island Press, Washington, D.C., USA.
- Manly, B. F. J., L. L. McDonald, and D. L. Thomas. 2002. *Resource selection by animals*. Second edition. Kluwer Academic, Dordrecht, the Netherlands.
- McGarigal, K., and B. J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. USDA Forest Service General Technical Report PNW-351, Front Royal, Virginia, USA.
- Miller, S. D., and D. W. Speake. 1979. Progress report: demography and home range of the bobcat in south Alabama. Pages 123–124 in L. G. Blum and P. C. Escherich, editors. *Bobcat research conference*

- proceedings. National Wildlife Federation Scientific and Technical Series 6, Front Royal, Virginia, USA.
- Millsbaugh, J. J., and J. M. Marzluff. 2001. Radio tracking and animal populations. Academic Press, San Diego, California, USA.
- Nielsen, C. K. 2000. Habitat use and population dynamics of bobcats in southern Illinois. Dissertation, Southern Illinois University at Carbondale, Carbondale, USA.
- Nielsen, C. K., and A. Woolf. 2001. Spatial organization of bobcats (*Lynx rufus*) in southern Illinois. *American Midland Naturalist* 146:43–52.
- Nielsen, C. K., and A. Woolf. 2002. Habitat–relative abundance relationship for bobcats in southern Illinois. *Wildlife Society Bulletin* 30:222–230.
- Pendleton, G. W., K. Titus, E. DeGayner, C. J. Flatten, and R. E. Lowell. 1998. Compositional analysis and GIS for study of habitat selection by goshawks in southeast Alaska. *Journal of Agricultural, Biological, and Environmental Statistics* 3:280–295.
- Phillips, M. L., W. R. Clark, M. A. Sovada, D. J. Horn, R. R. Koford, and R. J. Greenwood. 2003. Predator selection of prairie landscape features and its relation to duck nest success. *Journal of Wildlife Management* 67: 104–114.
- Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pages 65–103 in L. Boitani and T. K. Fuller, editors. *Research techniques in animal ecology*. Columbia University Press, New York, New York, USA.
- Prior, J. C. 1991. *Landforms of Iowa*. University of Iowa Press, Iowa City, USA.
- Preuss, T. S., and T. M. Gehring. 2007. Landscape analysis of bobcat habitat in the northern lower peninsula of Michigan. *Journal of Wildlife Management* 71:2699–2706.
- Ramsey, F. L., and D. W. Schafer. 2002. *The statistical sleuth: a course in the methods of data analysis*. Wadsworth Group, Pacific Grove, California, USA.
- Riley, S. P. D., R. M. Suvajot, T. K. Fuller, E. C. York, D. A. Kamradt, C. Bromley, and R. K. Wayne. 2002. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conservation Biology* 17:566–576.
- Rolley, R. E. 1983. Behavior and population dynamics of bobcats in Oklahoma. Dissertation, Oklahoma State University, Stillwater, USA.
- Rolley, R. E. 1987. Bobcat. Pages 671–681 in M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. *Wild furbearer management and conservation in North America*. Ministry of Natural Resources, Ontario, Canada.
- Rucker, R. A., M. L. Kennedy, G. A. Heidt, and M. J. Harvey. 1989. Population density, movements, and habitat use of bobcats in Arkansas. *Southwestern Naturalist* 34:101–108.
- Samuel, M. D., and M. R. Fuller. 1996. Wildlife radiotelemetry. Pages 370–418 in T. A. Bookhout, editor. *Research and management techniques for wildlife and habitats*. Fifth edition. The Wildlife Society, Bethesda, Maryland, USA.
- Seaman, D. E., J. J. Millsbaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gizen. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63:739–747.
- Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075–2085.
- Sunquist, M. E., and F. Sunquist. 2001. Changing landscapes: consequences for carnivores. Pages 399–418 in J. L. Gittleman, S. M. Funk, D. Macdonald, and R. K. Wayne, editors. *Carnivore conservation*. Cambridge University Press, New York, New York, USA.
- White, G. C., and R. A. Garrott. 1990. *Analysis of wildlife radio-tracking data*. Academic Press, San Diego, California, USA.
- Widner, R. R. 1968. *Forest and forestry in the American states, a reference anthology*. National Association of State Foresters, Missoula, Montana, USA.
- Woolf, A., and G. F. Hubert, Jr. 1998. Status and management of bobcats in the United States over three decades: 1970s–1990s. *Wildlife Society Bulletin* 26:287–293.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168.

Associate Editor: Conner.